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A Study of Senescence in the Red Raspberry Cane

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A STUDY OF SENESCENCE IN THE RED RASPBERRY CANE[1]

W. G. Brierley

INTRODUCTION

Many descriptions of the growth habit of the red raspberry plant *Rubus strigosus* appear in horticultural literature. Bailey (1) describes the raspberry as a plant with a perennial root and erect, or nearly erect, biennial canes. Under *Rubus* he says that in raspberries and blackberries the canes bear the second year and then die or become very weak. Darrow (4), Hedrick (11), and others, present similar descriptions. But in none of these is there any attempt to explain this behavior. Altho these writers do not discuss certain phases of the growth habit in detail, it is obvious that the apical meristem of the cane ceases to function at the end of the first year and that there are no winter buds formed on the cane in the second season. The development of the young cane, its behavior in the fruiting season, and subsequent decline and death are of necessity given consideration in numerous publications dealing with the practice of pruning. Apparently no attention has been given in these pruning studies either to radial growth or to the internal structure of the fruiting cane. As the structure and growth of the cane appear to have a relation to the fruiting performance and to pruning practices, the present studies were undertaken to determine the nature and extent of cambial activity and radial growth in the cane in the second year.

REVIEW OF LITERATURE

Apparently, there have been no reports upon the behavior of the cambium in the red raspberry in the second season, but studies of cambial activity and radial growth in other plants have a bearing on the subject. Hartig (9), writing in 1878, appears to have been the first to report upon the time of cambial activity in woody stems. From his studies, he concluded that in larch and maple cambial activity occurred first in the youngest twigs and then gradually extended downward, but that this behavior was not typical of some other trees. Gulbe (8) found that cambial activity in many species began with bud development, but that in some species this activity was delayed until the leaves were completely developed. Strassburger (29) stated that in

[1] Also submitted to the faculty of the Michigan State College of Agriculture and Applied Science in partial fulfillment of the requirements for the degree of Doctor of Philosophy, granted June, 1930.

general cambial activity begins in one-year shoots just back of unfolding buds and proceeds downward to the larger branches and trunks on which it usually begins uniformly and at about the same time from top to bottom. Jost (12) presented further evidence of this relation between bud development and cambial activity. Jost (13) later described the xylem development as a wedge-shaped strip of new wood, which gradually became thinner and finally disappeared in the direction of the stem base. This wood strip was largest below the strongest shoots, and in twigs with poorly developed shoots, very limited areas of new wood were formed. Mer (20) noted that cambial activity appeared first in the youngest twigs, but in certain cases was evident on one side of the twig and not on another. Reiche (23) showed that radial growth of trees did not occur unless bud development preceded it. Lutz (17) also indicated that the initiation of new growth is from above downward, but showed further that branches of young trees of certain species disbudded in March remained healthy but with no radial growth. Hastings (10) found the first new wood was formed in the neighborhood of terminal buds and was not continuous around the stem. Simon (25) concluded from similar studies that in certain woody species secondary thickening spread downward very slowly. Pfeffer (21) found that the secondary growth of xylem in trees began and ended sooner than that of the phloem. Knudson (15), however, found that in the American larch new phloem was formed before new xylem appeared, but the greatest growth of phloem coincided with the greatest development of xylem. Grossenbacher (7) in 1915 presented an excellent review of the literature relating to radial growth, in which he showed that in general cambial activity begins in young shoots just back of unfolding buds and proceeds downward to the older parts of the plant.

Few reports relating to cambial activity of fruit plants appear in the literature. Knudson (16) found that in the grape new phloem and xylem were formed simultaneously, the cambium becoming active when the leaves were almost completely developed. In the apple, this activity was found to be similar to that of the grape in that it was preceded by considerable leaf development. In the peach, cambial activity was found to begin with the opening of the buds. Knight (14) showed that in the apple cambial activity was very similar to that of other woody plants, in that new xylem was formed first in the region bearing developing buds, and that wherever bud-growth occurred new xylem formation invariably accompanied it. This activity proceeded downward into "bare" regions of the stem in which buds had not developed. Swarbrick (27) also found that in the apple, xylem differentiation began in the terminal region of shoots and spurs and progressed downward towards the roots. He observed that at the base of one-year-old shoots the first xylem differentiation was down the sides of the "vascular bundles," and that the vigorous development of a spur on a short lateral branch resulted in early xylem formation in the branch on the side corresponding to the point of spur insertion. Swarbrick (28) later showed that there was no cambial activity in areas on an apple shoot, which were isolated by a double girdle and disbudded. When buds remained and developed, xylem formation was found to be proportionate to the vigor of the shoot. In disbudded isolated areas, the cambium lost its meristematic condition by September and xylem was not formed at any time. Sledge (26) found that in hardwood cuttings of the apple and other species cambial activity not only spread downward from the tips due to the stimulus from developing shoots, but also spread upward from the proximal ends. He attributed this latter type of cambial activity to a stimulus from the wound at the base of the cutting.

As previously stated nothing appears in the literature in relation to cambial activity in the raspberry. However, in some studies of the behavior of the European blackberry, Bonnier (3) found that some canes could be kept alive into the third and fourth seasons, by trellising them in a vertical position. Altho he noted a marked decline in vigor of growth he found that a ring of new wood and phloem was formed in some of these canes in the third season, but this ring was much narrower than the rings formed in the first and second years. MacDaniels (18), in his studies of fruit bud formation in the genus *Rubus,* found that when old canes of the Herbert raspberry were disbudded they generally died, but disbudded old canes of the Snyder blackberry generally lived and frequently produced fruiting laterals. In the present studies some old canes of the Latham variety which were disbudded in early spring died and dried up by midsummer. This behavior of the raspberry is in marked contrast to that of the woody species studied by Lutz (17). Bennett (2) attempted to transmit virus diseases in the raspberry by budding and bark grafting, but found it extremely difficult to obtain successful unions. The present studies show that the cambial activity of the red raspberry cane in the second season is much the same as that of other woody stems, but that this activity in general is feeble.

DEFINITION OF TERMS USED IN RELATION TO THE CANE AND ITS PARTS

In descriptions of the raspberry plant, or of its horticultural varieties, or in discussions of pruning there is some confusion in regard to the names given to the various parts of the cane. In order to avoid this confusion, the following definitions are offered, covering the terms used in these studies:

Young cane.—The new growth usually arising as suckers from the root, or from the underground portion at the base of an old cane. In some localities these new canes are called "turions." With regard to season, the young cane is considered to continue through the winter until the end of the dormant season. On the young cane, winter buds are developed from which lateral shoots arise in the second year.

Old cane.—The cane from the beginning of growth in the second year until the end of that season, when the cane usually dies. Growth of the old cane results chiefly in the production of leafy lateral shoots on which the flowers and fruits are borne. Under normal conditions no terminal growth occurs in the second year and no winter buds are developed either on the cane or laterals.

Branch.—A division of the young cane, developed in the first year. Essentially the same as a young cane, but arising from it instead of from the crown or root.

Lateral.—A leafy shoot of the old cane or branches developing from a winter bud and usually bearing flowers and fruits. Many of the laterals may produce neither flowers nor fruits. To distinguish between them on the basis of performance they may be called fruiting laterals or barren laterals.

INCREASE IN DIAMETER OF OLD CANES

Observations of old canes of the red raspberry do not as a rule reveal any material increase in diameter in the second season. In some cases, as shown in Figure 1, an increase in cane diameter is readily discernible below vigorous laterals. Bonnier (3) found narrow "annual rings" formed in the second and third seasons in specially handled blackberry canes, but nothing has been found in the literature to show that raspberry canes behave in this way. To obtain some detailed evidence on this phase of the problem, measurements were made of dormant young canes and of old canes at the end of the second season. Beginning 1 cm. above the ground, measurements were made with a vernier caliper at 5 cm. intervals up to the tips of each cane. The average of two measurements taken at approximately right angles to each other was used as the diameter at each height. The canes were arbitrarily placed in three classes with regard to diameters at the base as follows:

(1) Vigorous canes, above 1.25 cm.; (2) medium canes, from 1.00 to 1.25 cm.; (3) weak canes, less than 1.00 cm. The average diameters for the dormant young canes are given in Table I. The measurements of the available old canes are given in Table II. The data from these tables are shown graphically in Figure 2.

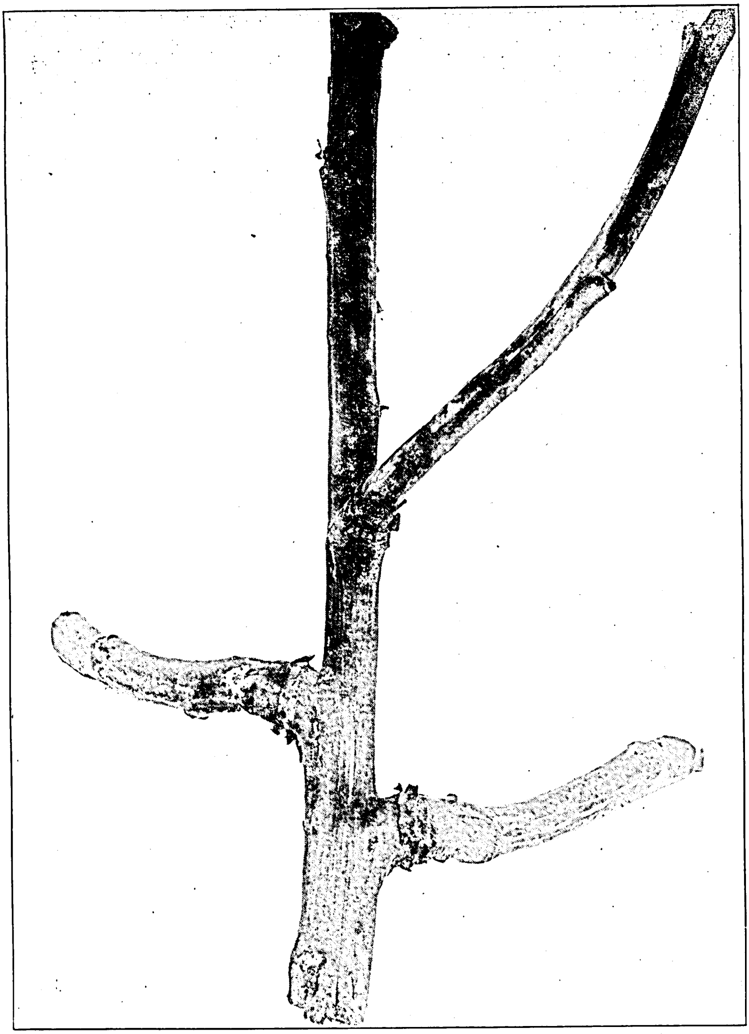

Fig. 1. Old Cane Showing Obvious Increase in Diameter Just Below Vigorous Laterals

Altho the number of canes in each class was not large and no old canes were available with a diameter of more than 1.25 cm. at the base, the data indicate that the red raspberry cane generally does increase in diameter in the second season. The diameters of the dormant young canes decline very regularly from the base upward, regardless of cane vigor. The old canes show a slight increase in diameter for a distance of about 25 cm. from the base. Beyond that point the diameters decline more or less regularly with increasing height. Measurements of the old canes at hand could not be made up to the same height as the new canes because of tip pruning. Comparisons between the

TABLE I

DIAMETERS OF NEW CANES AT SUCCESSIVE HEIGHTS

Height above ground in cm.	Vigorous		Medium		Weak	
	No. canes	Average diameter in cm.	No. canes	Average diameter in cm.	No. canes	Average diameter in cm.
1	15	1.42	18	1.12	18	0.89
6	15	1.38	18	1.05	18	.85
11	15	1.34	18	1.02	18	.81
16	15	1.30	18	.99	18	.79
21	15	1.27	18	.97	18	.77
26	15	1.25	18	.96	18	.75
31	15	1.23	18	.93	18	.72
36	15	1.20	18	.91	18	.70
41	15	1.17	18	.89	18	.68
46	15	1.15	18	.87	18	.66
51	15	1.12	18	.85	18	.64
56	15	1.09	18	.83	18	.61
61	15	1.08	18	.80	18	.58
66	15	1.05	18	.78	18	.57
71	15	1.03	18	.75	16	.56
76	15	1.01	18	.73	16	.54
81	15	.98	18	.70	16	.52
86	15	.95	18	.68	15	.51
91	15	.91	18	.65	14	.50
96	15	.90	18	.64	13	.48
101	15	.86	18	.62	10	.48
106	15	.83	17	.61	10	.44
111	15	.80	17	.58	10	.41
116	15	.77	17	.55	10	.39
121	15	.74	16	.51	10	.37
126	15	.72	15	.49	8	.36
131	15	.68	13	.47	6	.33
136	15	.64	12	.45	—	—
141	12	.64	10	.44		
146	12	.59	10	.40		
151	10	.61	9	.39		
156	10	.57	6	.41		
161	10	.53	5	.39		
166	9	.51	4	.37		
171	9	.49	—	—		
176	9	.47				
181	8	.45				
186	7	.42				
191	6	.41				
196	6	.39				

old and young canes of the same relative vigor show that the old cane has a small but constant advantage in diameters except at the base. This relation is shown clearly in Figure 2. These data indicate that, in the average old cane, radial growth occurs in the central and upper portions but not at the base close to the ground.

Further evidence of the failure of the old cane to increase in diameter at the base was obtained by examining the tissues exposed in cross-section when canes of this age were cut off at the ground. Old canes of Cuthbert and Latham from several sources were examined in this manner, by means of a hand lens of suitable magnifying power. In doubtful cases a free-hand section was cut from the base of the

TABLE II

DIAMETERS OF OLD CANES AT SUCCESSIVE HEIGHTS

Height above ground in cm.	Vigorous		Medium		Weak	
	No. canes	Average diameter in cm.	No. canes	Average diameter in cm.	No. canes	Average diameter in cm.
1	*	*	25	1.08	30	0.85
6			25	1.09	30	.86
11			25	1.10	30	.87
16			25	1.09	30	.87
21			25	1.09	30	.87
26			25	1.08	30	.85
31			25	1.07	30	.84
36			25	1.04	30	.83
41			25	1.01	30	.81
46			25	.99	30	.80
51			25	.96	30	.78
56			25	.95	30	.76
61			25	.92	29	.74
66			25	.91	28	.74
71			25	.87	28	.71
76			25	.84	26	.68
81			25	.80	21	.67
86			23	.77	17	.66
91			21	.74	12	.67
96			17	.72	10	.66
101			10	.69	6	.65
106			6	.74	6	.61
111			4	.72	—	—
116			3	.65		

* None available.

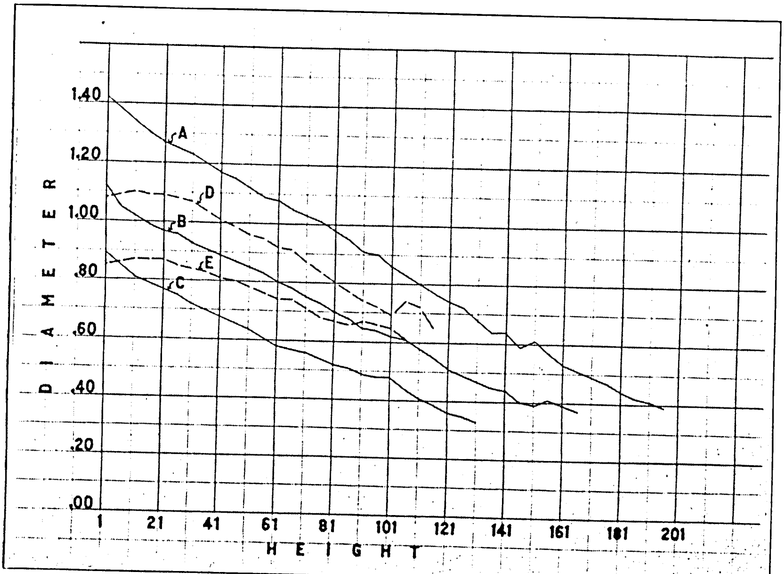

Fig. 2. Diameters at Successive Heights in Young and Old Canes

A. Vigorous young canes; diameter at base greater than 1.25 cm.
B. Young canes of medium vigor; diameter at base from 1.0 to 1.25 cm.
C. Weak young canes; diameter at base less than 1.0 cm.
D. Old canes of medium vigor; similar to B.
E. Weak old canes; similar to C.

cane and examined under a binocular microscope. For convenience in tabulating the data, all canes less than 1 cm. in diameter at the base were classed as weak and all of greater diameter classed as vigorous. These data are shown in Table III.

TABLE III

OCCURRENCE OF NEW XYLEM AT THE BASE OF OLD CANES

Variety and source	Vigorous canes (More than 1 cm. in diameter at base)				Weak canes (Less than 1 cm. in diameter at base)			
	Present	Per cent	Absent	Per cent	Present	Per cent	Absent	Per cent
Cuthbert, Mich.	18		56		15		77	
Cuthbert, Mich.	0		93		1		63	
Cuthbert, Wash.	1		21		0		30	
Total	19	10.0	170	90.0	16	8.6	170	91.4
Latham, Mich.	11		11		7		92	
Latham, Minn.	4		30		0		82	
Latham, Minn.	8		33		2		11	
Total	23	23.7	74	76.3	9	4.6	185	95.4
Total	42	14.7	244	85.3	25	6.6	355	93.4
Total, all canes both varieties	67	10.1	599	89.9				

Table III indicates that in slightly more than 10 per cent of the old canes examined new xylem was found at the base ranging in amount from a few scattered vessels and fibers up to well developed complete rings. New xylem was found more frequently in vigorous canes (14.7 per cent) than in weak canes (6.6 per cent). Very little difference was found between vigorous and weak canes in the Cuthbert variety, but vigorous canes of the Latham showed new xylem occurring much more frequently (23.7 per cent) than weak canes (4.6 per cent). The difference between the two varieties is thought to be due to the greater tendency of Latham canes to develop vigorous laterals near the base. In some unpublished studies of the effect of various pruning heights upon cane behavior in the Latham, the writer has found that basal laterals originating within 1 to 5 cm. from the ground quite frequently grow to a length of 100 cm. or more. Occasionally these laterals are barren and develop into new canes ranging from 150 to 200 cm. in height. In cases of this kind a well-developed complete ring of new xylem has been found at the base. This type of growth has been observed in the Cuthbert, but does not appear to be as common.

As only one out of 10 old canes apparently has new xylem at the base, and as little or no new phloem is formed close to the ground in the average cane (as will be shown later), it is obvious that the majority of old canes depend almost entirely upon old tissues for the conduction of water and foods through the basal region. It is considered possible that this condition at the base may in part explain the fact that old canes generally are less vigorous than young canes.

INTERNAL ANATOMY

Materials and Methods

In these studies, sections were cut from both young and old canes in the fresh condition, without killing or embedding the material. The sections were cut about 20 to 30μ in thickness, with a slide microtome. The canes were found to be firm enough to handle in this manner if, when the microtome clamp was adjusted, care was exercised not to crush the shell of wood surrounding the extensive area of pith. The staining of this material was found to be most satisfactory when a one per cent aqueous solution of safranin was used in combination with Delafield's hematoxylin. These stains usually produced the most satisfactory results when somewhat diluted. Better results also were obtained when the hematoxylin was used before the safranin. The usual procedure was followed with regard to dehydrating in alcohol and clearing in xylol. Neutral Canada balsam was used for mounting the material. At times it was found difficult to hold the safranin stain in the xylem. Apparently the xylem region was sufficiently acid in reaction to cause the bleaching of the stain soon after mounting. This difficulty was avoided to a considerable extent by using in one stage of the dehydration process 95 per cent alcohol to which a few drops of a dilute solution of sodium hydroxide were added.

Most of the cane material for these studies was obtained from the Latham and Cuthbert varieties from various sources in Michigan and Minnesota. Some use was made of canes of the Ranere (St. Regis) variety obtained from Ohio, Illinois, and Washington, D.C. For purposes of comparison, some canes of the Cuthbert raspberry and the Evergreen and Logan blackberries were obtained from western Washington.

In a majority of cases, when canes were examined, sections were made from four general regions of the cane. The first sections were cut as close as possible to the base; others were then cut from a point 5 to 10 cm. higher up on the cane, from the central region of the cane, and from the tip region. Transverse, radial, and tangential sections were made at each point. It was found during the progress of the work that the evidence relating to radial growth was shown most clearly in the transverse sections, so this form was emphasized in the later work. Transverse sections were made from some old canes at 5 or 10 cm. intervals from the base to the tips, to ascertain the location and extent of development of new xylem.

In the process of sectioning, the pith was found to crush or tear away if the sections were cut sufficiently thin to be of value. Also the loose outer layers of the periderm usually were torn off. However, the loss of these portions of the sections was not serious as the studies deal mainly with the cambium and adjacent tissues.

Resting Cambium

From studies of the dormant young cane and of old canes at the beginning of the growing season, it appears that the cambium is in the resting condition noted by Roberts (24) in some apple seedlings. Figures 3 and 4 illustrate this condition in the dormant young canes of Ranere and Cuthbert.

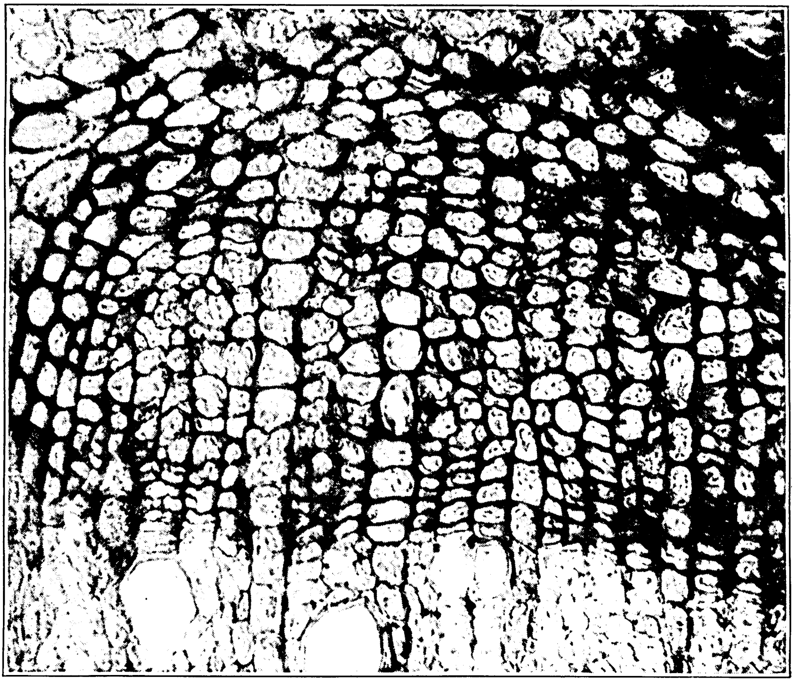

Fig. 3. Cross-section from the Base of a Ranere Cane in March Showing Resting Cambium. ×435

Response of Cambium to the Stimulus from Developing Buds

The cambium in the old cane seems to respond very slowly and feebly to the stimulus from developing shoots. Examinations of old canes from plants grown in the greenhouse indicate that the cambium in the cane generally did not become active until the laterals were well developed. In vigorous canes, particularly from plants fertilized with a moderate application of sodium nitrate just before the buds opened, some cambial activity was found when the laterals, with several partially unfolded leaves, were not over 5 cm. in length. This activity, as evidenced by the formation of new xylem, was feeble and occurred only immediately below the most vigorous laterals. Figure 5 shows this condition in the central region of a Cuthbert cane. In other canes, particularly those making a weak growth in the second season, cambial activity was not apparent even when the laterals were 20 cm. in length, with several well-developed leaves and with the blossom buds appearing. Figure 6 illustrates this condition in the tip region of a Cuthbert cane.

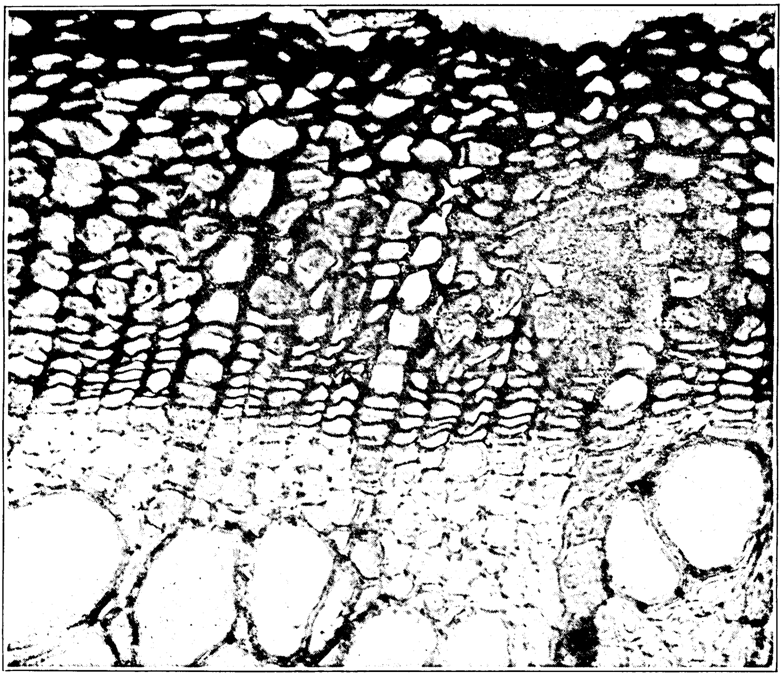

Fig. 4. Cross-section from the Base of a Cuthbert Cane in March Showing Resting Cambium. ×435

The development of cambial activity in response to the stimulus from growing laterals appears to proceed down the cane very slowly and is markedly feeble at a point only a few centimeters below a lateral. Even in vigorous canes the activity of the cambium a short distance below a lateral appeared to be restricted in many cases to an increase in the radial diameters of the cambial cells. The cambium at these points, also, seems to have failed to maintain its width, indicating that some of the outer cells had differentiated into phloem elements, but that no new cambial cells were formed. This condition is shown in Figure 7.

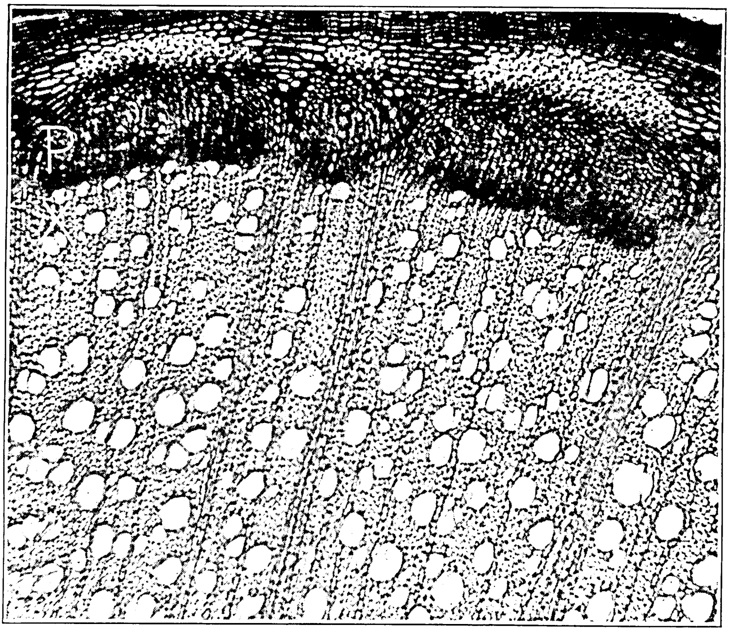

Fig. 5. Feeble Activity of the Cambium Just Below a Vigorous Young Lateral from the Central Region of a Cuthbert Cane

New xylem (X) very limited in amount. Darker staining of the inner phloem (P) indicates that these cells are of recent development. ×96.

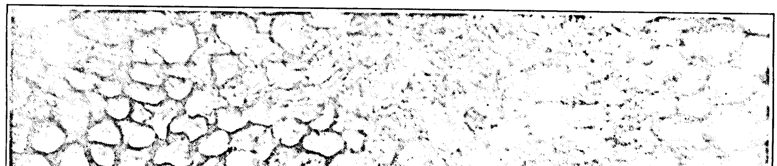

Fig. 6. Cambium Just Below a Well-developed Lateral with Blossom Buds Appearing From the tip region of a weak Cuthbert cane. No activity apparent. ×435.

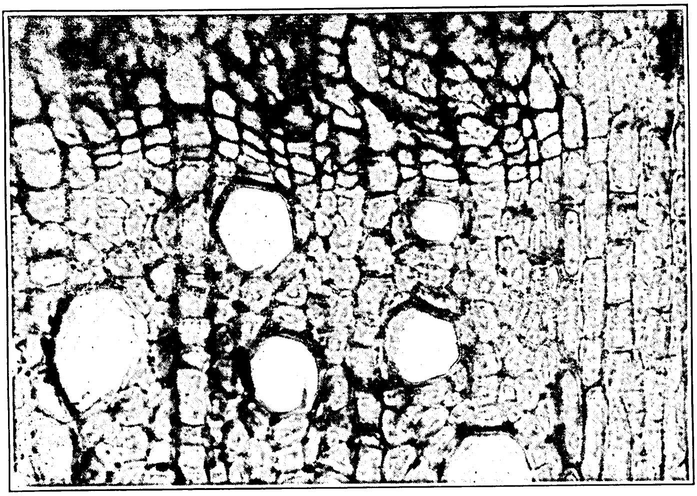

Fig. 7. Cambium from the Central Region of a Cuthbert Cane, 5 cm. Below a Vigorous Lateral with First Blossoms Open

Feeble activity evidenced by reduction in width of cambium and an increase in radial diameter of the cells. ×435.

Altho in the majority of old canes the cambium in the basal region appears to remain in the resting condition when no laterals develop in that region, a feeble development similar to that noted above was found in some canes which did not develop vigorous laterals near the ground.

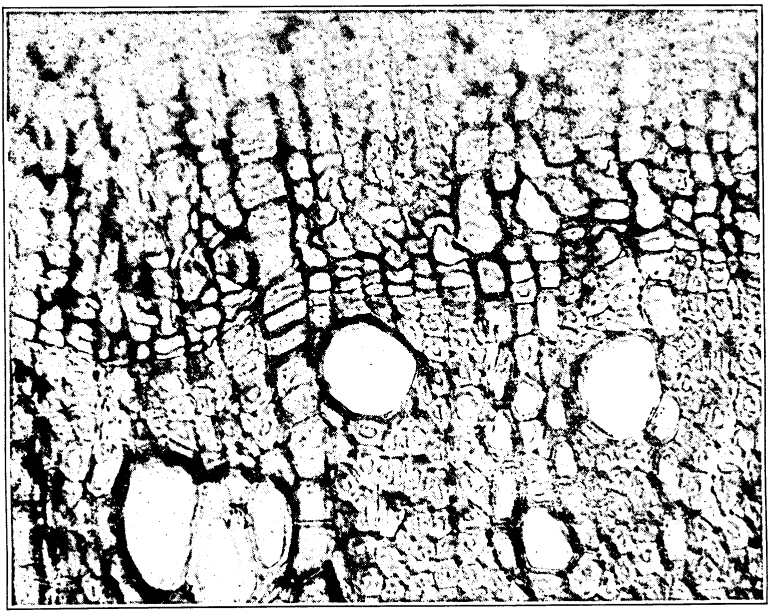

Fig. 8. Cambium at the Base of a Cuthbert Cane Showing Feeble Activity Similar to That Shown in Figure 7. ×435

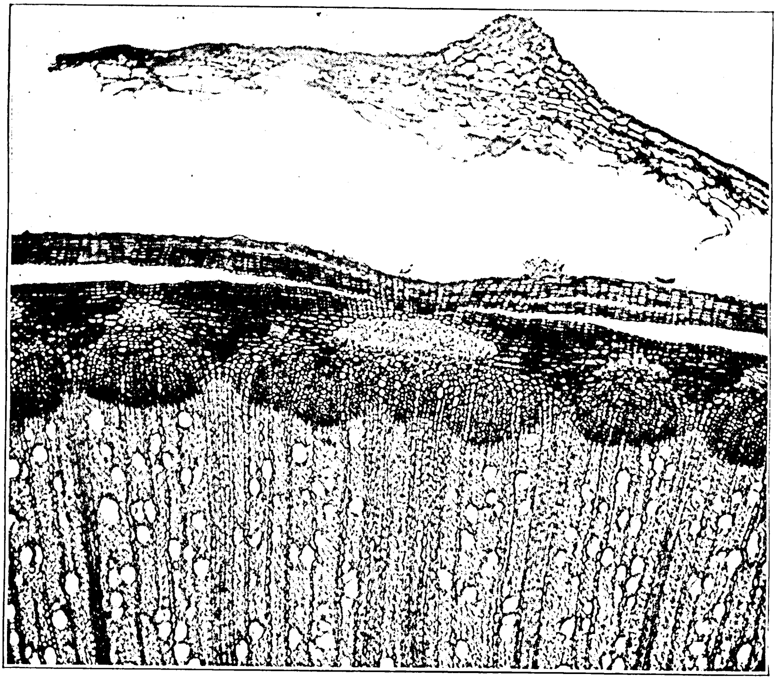

Fig. 9. Irregular Margin of the Xylem at the Base of a Cuthbert Cane Sectioned just before bloom. Suggests the possibility that senile decline of the cambium begins sometime in the first season. ×96.

Figure 8 illustrates this condition at the base of a vigorous cane of the Cuthbert variety. In the Evergreen blackberry no cambial activity was noted in the basal region of the few canes examined, and no new xylem was formed in the second year. This condition is shown in Figure 10.

The slow response and feeble development may be considered indications of senile decline in the raspberry cambium. That this decline may begin toward the close of the previous growing season, is suggested by the irregular margin of the xylem in the dormant young cane (see Figures 9 and 20), altho some disturbance in relation to the kind or quantity of available food substances possibly may have produced this effect. This irregular development of the xylem areas between the aggregate rays was more noticeable in the Evergreen blackberry in the few canes examined, as shown in Figure 10. Altho the difference in radial growth of the xylem in these areas usually did not amount to more than 8 or 10 cells, it is considered possible that this difference is the result of earlier cessation of cambial activity in some areas. This somewhat erratic behavior of the cambium suggests the possibility that it was approaching the condition of senility, which is more evident in the old cane in the second season. Further evidence

Fig. 10. Base of an Evergreen Blackberry Cane at the End of the Second Year
Shows resting cambium (C), wider area of active phloem (P) than in the red raspberry, and a markedly irregular margin of the xylem (X). No new xylem was formed. ×96.

of this decline will be presented in the discussion of the behavior of stem cuttings.

Development of New Xylem in the Old Cane

The most obvious result of cambial activity in the old cane in the second season is the formation of new xylem. That the old canes generally do increase in diameter in the central and tip regions but usually not at the base has been discussed. Studies of the anatomy of the old cane show the presence of new xylem in varying amounts in the regions which normally increase in diameter. The formation of new xylem elements was found to occur first just beneath a rapidly growing lateral and proceeded downward slowly from that point.

The amount of new xylem formed during the second season was much more extensive immediately below the laterals and on the same side of the cane. The areas of new xylem as seen in cross-section were greatly reduced or entirely absent on other sides of the cane (Fig. 12). This localized development often produced two, well-marked, but short ridges extending downward from the sides of the base of the lateral. Generally these "ridges" of xylem, which cor-

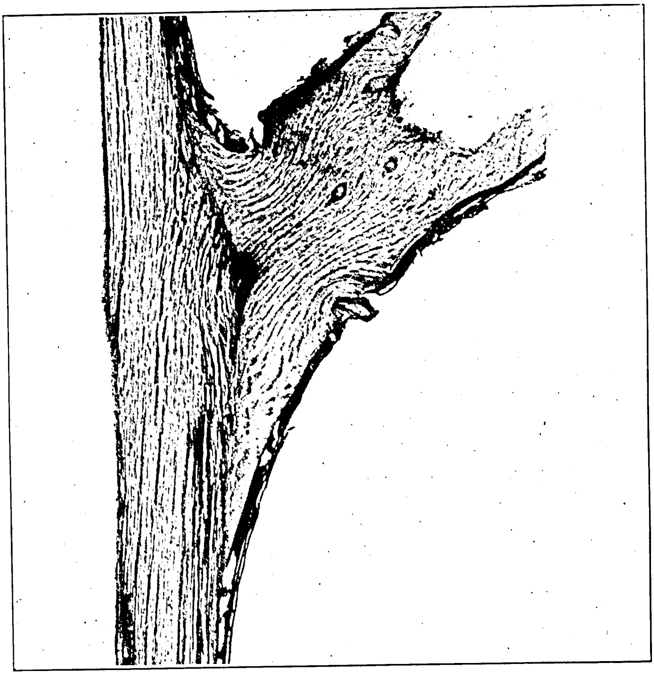

Fig. 11. Longitudinal Section Made in December Through the Base of a Lateral on a Vigorous Old Cane of the Latham Variety

"Wedge" of new xylem tapers to a point within 2 cm. below the point of bud insertion. Phloem in collapsed state. Pith and opposite side of old cane torn away in sectioning. ×6.

respond to the "wedges" described by Jost (13), continue for only a very short distance below the laterals. Figure 11 shows a longitudinal section through one side of a cane at the point of attachment of a vigorous lateral. This illustrates the rapid tapering of the wedges of new xylem. The distance from the point of bud insertion to the end of this wedge was not over 2 cm. The cross-sections shown in Figures 12, 13, 14, 15, and 16 were made at the base of a similar lateral, beginning at the point of bud insertion and progressing downward at 0.5 cm. intervals. These sections show the rapid narrowing of the wedges. The last of this series (Fig. 16), cut at a distance of only 2 cm. below the point of bud insertion, shows very narrow areas of new xylem in an incomplete ring.

The very limited development of new xylem at the base of the laterals provides a very weak attachment to the old cane and doubtless explains why the laterals are so easily broken off in cultivation and in picking, or in severe storms.

In canes which did not develop laterals close together, the stimulus

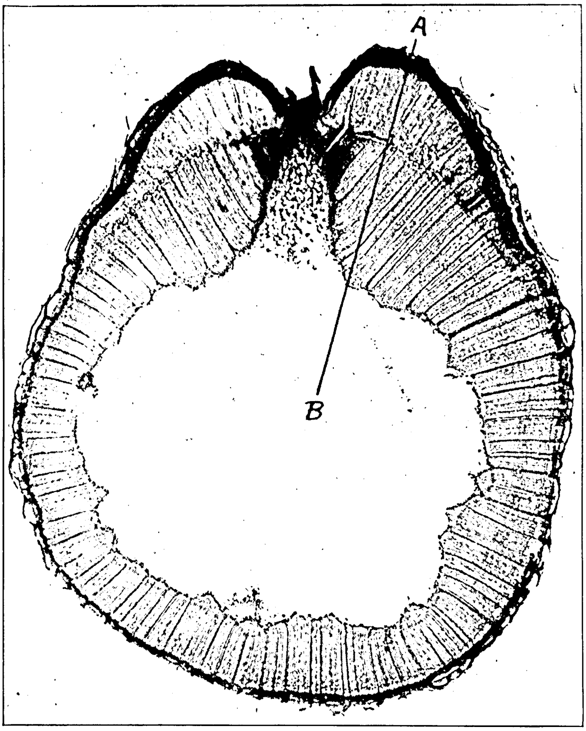

Fig. 12. Cross-section Through the Base of a Vigorous Lateral from the Same Cane as Figure 11

Section made at about the point of bud insertion. Note prominent "ridges" and the rapid narrowing of the area of new xylem. New ring incomplete. The line A-B indicates the approximate location of the section shown in Figure 11. ×6.

from the growing laterals apparently did not progress to any great distance down the cane. At the time of fruit-ripening, sections made 5 cm. below vigorous laterals often showed only a few scattered vessels and fibers, and in many cases there was no evidence to show that new xylem had been formed. Figure 17 shows a cross-section cut just beneath a lateral from a Cuthbert cane when the fruit was ripening. In this case new xylem was formed in some quantity at this point, but no evidence of new xylem formation could be found at a point only 5 cm. below.

When numerous laterals were developed fairly close together in the central and tip regions of a cane, the formation of new xylem was general around the cane. Altho a complete ring of new xylem may be formed under these conditions, as shown in Figure 18, this ring generally was very narrow and often was incomplete as shown in Figures 12 to 16. This very limited development of new xylem explains why

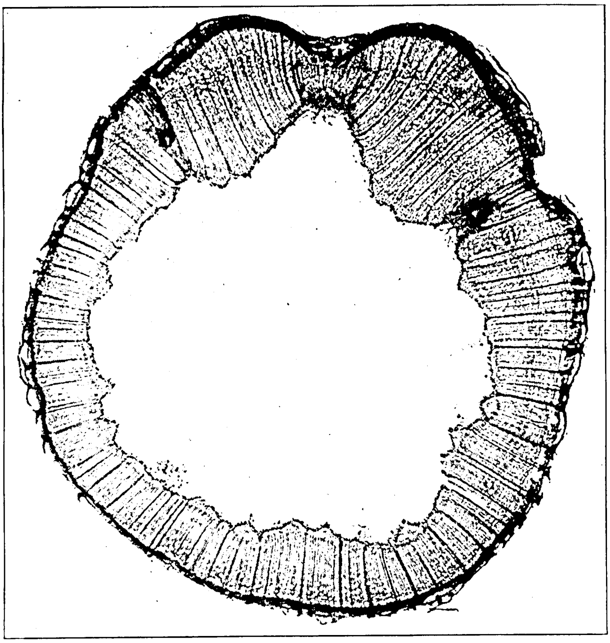

Fig. 13. Section Cut .5 cm. Below Figure 12. ×6

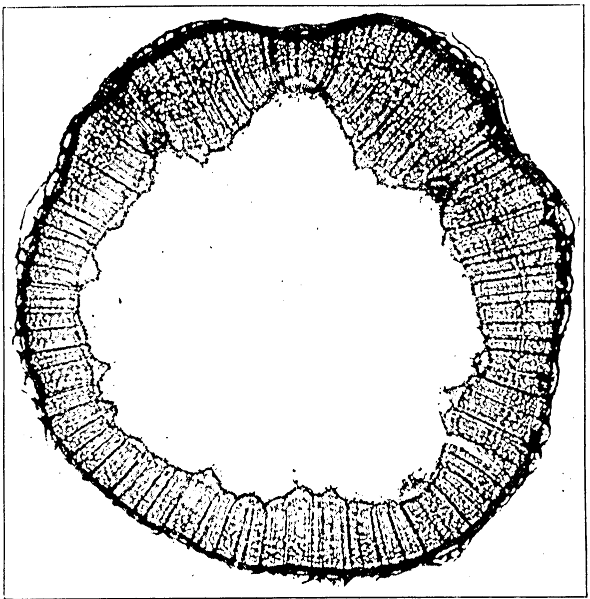

Fig. 14. Section Cut 1 cm. Below Figure 12. ×6

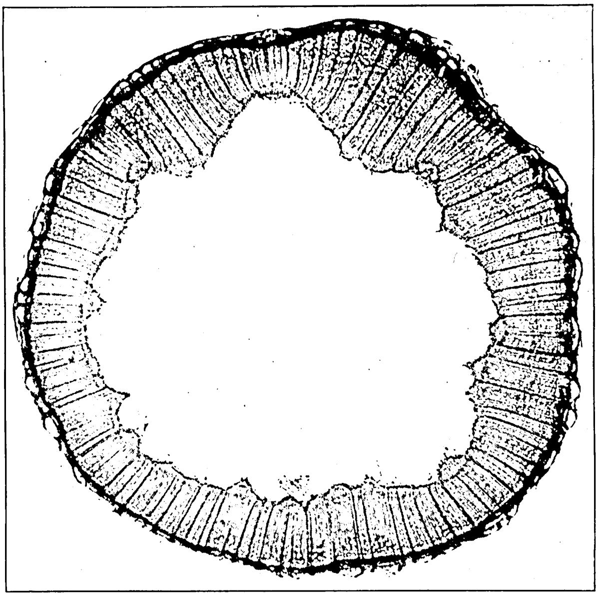

Fig. 15. Section Cut 1.5 cm. Below Figure 12. ×6

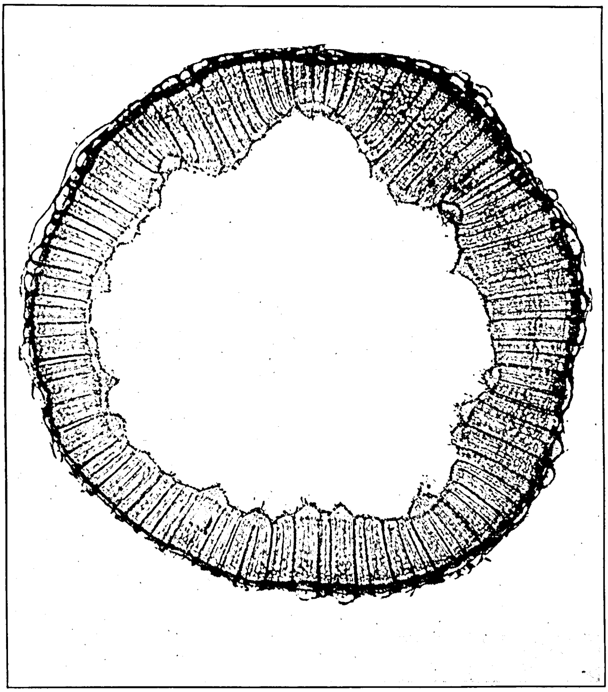

Fig. 16. Section Cut 2 cm. Below Figure 12. This and the Three Preceding Figures Show the Rapid Narrowing of the Wedges of New Xylem Below a Lateral. ×6

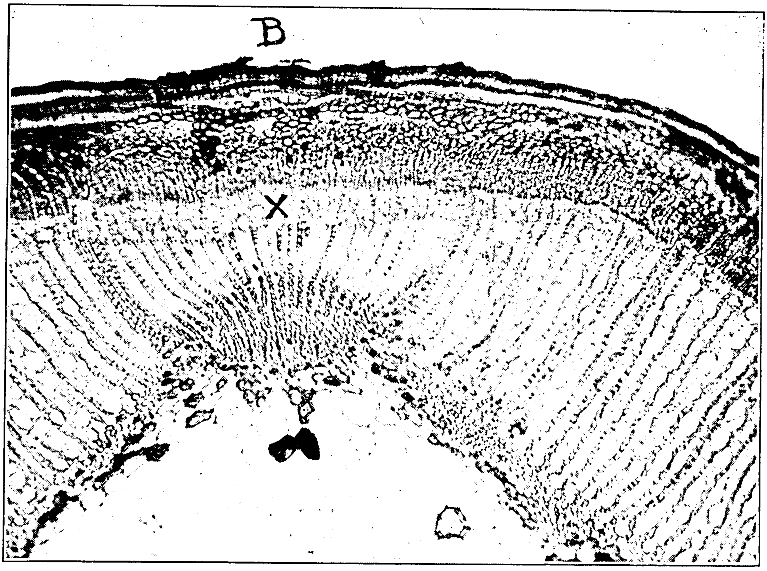

Fig. 17. Cross-section Made Just Below a Lateral of Medium Vigor in the Tip Region of a Cuthbert Cane

No other laterals within 15 cm. Fruit nearly all harvested. New xylem (X) in greatest area just below the point of bud insertion (B). "Ring" narrowing rapidly and absent over a large part of the opposite side of the stem. No trace of cambial activity 5 cm. below the lateral. ×96.

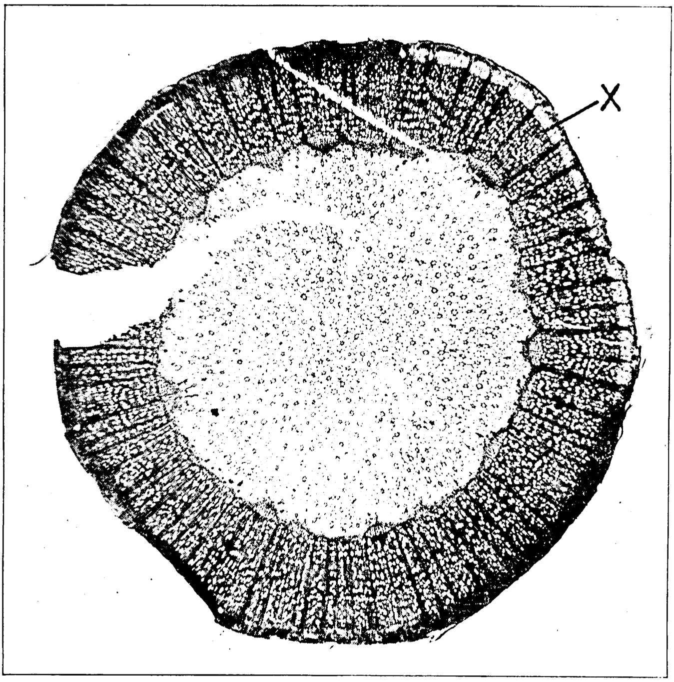

Fig. 18. Complete Ring of New Xylem (X) in Central Region of Latham Cane with Many Vigorous Laterals. ×6

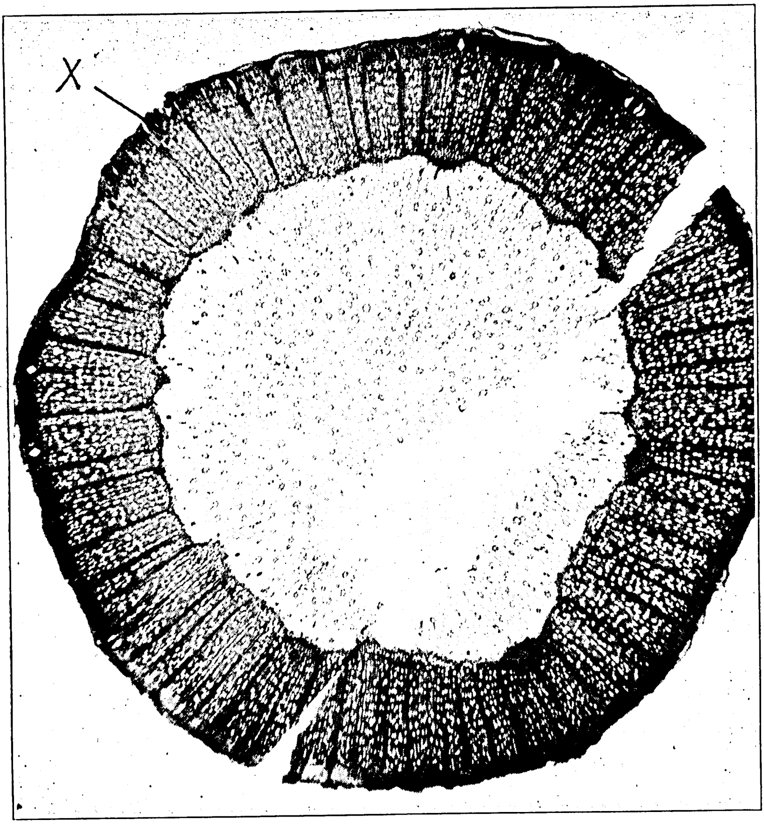

Fig. 19. Complete Ring of New Xylem (X) at the Base of a Latham Cane Sectioned in November after the fruiting season. Several vigorous laterals were present in the basal region of this cane. X6.

there is such a slight increase in diameters throughout the length of the old cane. This slight increase occurred, however, even at the very tip of the cane, providing fairly well-developed laterals were present.

It is apparent from the foregoing evidence that the general, altho feeble, development of new xylem, which causes the increase in diameter in the upper regions of the cane, is caused by the cumulative effect of the stimulus from many laterals upon cambial activity.

The average cane does not produce many laterals in the basal region. Usually there are no laterals within 10 to 15 cm. from the ground. In the absence of basal laterals, the stimulus from laterals higher up on the cane apparently does not proceed downward far enough to affect the cambium at the base. Because this stimulus is lacking, the cambium at the base remains in a resting condition, or nearly so, and no new xylem is formed (Fig. 8). Without the formation of new xylem no measurable increase in diameter occurs at this point. However, when vigorous fruiting laterals developed in the basal region, as noted previously with regard to the performance of the Latham variety, new xylem was found in this region, but the area commonly was not extensive and the "ring" often incomplete. When these basal laterals were extremely vigorous, or when they were sterile and developed into new canes, the new xylem often formed a complete ring, which in some cases was of considerable width, as shown in Figure 19. This occurrance of new xylem explains the increase of diameter at the base in about 10 per cent of old canes.

Xylem formation has been shown to be more abundant just below a vigorous lateral than below a lateral of medium vigor. Some data obtained at the Minnesota Experiment Station, relating to the effects of pruning on cane behavior, show that canes pruned to a height of 36 inches produced longer and stouter laterals than canes pruned to a height of 60 inches. The shorter canes when examined showed a slightly larger amount of new xylem than the longer canes, but these shorter canes suffered more severely from storm damage to the laterals. In a series of plots, grown in staked hills and equally exposed to storm damage, the 36-inch canes showed an average of 12.9 per cent of the laterals broken off, whereas in the 60-inch canes the loss from breakage was only 9.2 per cent. It is apparent from these data that the increase in the vigor of the laterals on the shorter canes did not result in an increase in the strength of attachment to the cane sufficient to support the longer growth against the additional wind leverage.

Development of New Phloem in the Old Cane

The evidence obtained relative to phloem formation in the old cane is neither so clear nor so extensive as that relating to new xylem. Where new xylem was found in the old cane it was often accompanied by an area of phloem adjacent to the cambium, which stained noticeably darker, as shown in Figures 5, 17, and 20. This darker stain indicates that these cells are of more recent development with denser protoplasm than cells farther out in the phloem area. A more detailed study of these cells showed them to be filled with dense (heavily stained) protoplasm, whereas cells farther out were often empty. Some of the darker-stained cells may have been differentiated late in the previous growing season and remained in an active condition. This apparently is the condition also found in the Evergreen blackberry (Fig. 10). Others possibly were formed from the cambial initials late in the previous season, but were not completely differentiated until the start of the second year. Eames and MacDaniels (6) (p. 155) state in regard to the differentiation of phloem: "There is evidence to show that the cambial derivative cells first to mature in the

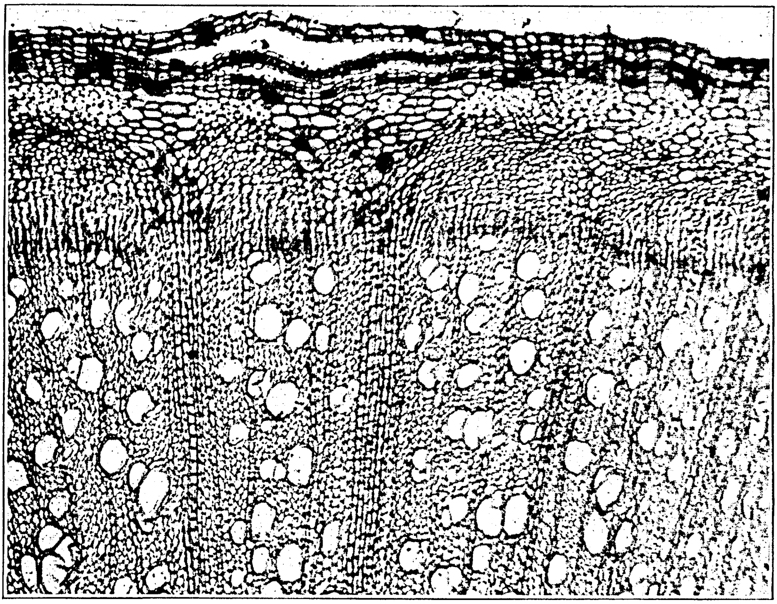

Fig. 20. Cross-section of Tip Region of Cuthbert Cane

Laterals 8-10 cm. long and blossom buds about ready to open. Cambium apparently inactive. Narrow area of phloem (P) adjacent to the cambium stained darker than remainder. Margin of xylem somewhat irregular. ×96.

spring are phloem mother cells. Of these, at least a part were cells which were cut off from the cambial initials during the previous season and have remained over winter in an immature condition." It has been shown already that the cambial area in some cases is reduced in width, altho the cambium showed no marked indications of activity (Figs. 7 and 8). This is considered evidence that some phloem cells are matured in the second year without division of the cambial initials at that time. Still others of the darker-stained phloem cells probably were the result of cambial activity in the second season.

Knudson (16) noted that in the grape and apple new xylem and phloem were formed simultaneously. This may also be the type of behavior in the red raspberry, as the darker-stained areas shown in Figures 5 and 20 appear to be wider than would be accounted for by the differentiation in the spring of a few immature cells cut off from the cambial initials at the close of the previous season. Altho the probability exists that the outer portions of this area may have been made up of cells which were differentiated late in the previous season and remained in an active condition, it is also probable that some of the innermost cells may have been formed by the division of cambial initials at the same time that new xylem cells were formed.

This phloem area regardless of time of formation was relatively narrow, being comparable in that respect to the narrow area of new xylem ordinarily found in old canes. As it appears probable that only a part of this narrow area was formed from the cambial initials in the second season, this may be considered further proof of the feeble activity of the cambium in the old canes.

Decline of the Phloem

Numerous examinations of old canes showed that the phloem began to break down at about the height of the harvest season. In Cuthbert plants, grown in the greenhouse, browning of the phloem at the base of the old canes was found to begin when about half of the fruits had ripened. In field-grown plants of King and Latham no discoloration was noted until most of the crop had matured. This discoloration occurred a little earlier in the season in the King than in the Latham, but the fruiting season of the King is also earlier than the Latham. Toward the end of August when the foliage of the old canes was beginning to turn yellow and terminal growth of the young canes had almost ceased, the browning of the phloem at the base of the canes was more noticeable. In early September the browning was more pronounced, but at that time there was no indication of collapse of the cells. The browning was intensified by the end of September, and, in canes examined in November after the leaves had fallen, the phloem was almost completely broken down and the cells were often collapsed. This condition is shown in Figures 11 and 21.

The breakdown of the phloem appeared to occur first at the base of the canes, a region in which little or no cambial activity in the second season was found. In the central region of the canes the phloem did not discolor until some time later than at the base. In many of the canes examined the phloem in this region was apparently normal in late August. Degeneration of the phloem in the tip region of the canes appeared to occur at about the same time as at the base. In some cases the tip region was the first to show this discoloration. This condition at the tips is thought to be caused by some disturbance in the water supply of the region, as that part of the cane often shows signs of drouth injury, while the lower portions are not affected as much. The cambium in the tip region has been shown to be fairly active, so it appears that the degeneration of the phloem in this region is not due to the same cause as degeneration at the base, where the cambium is inactive as a rule. Altho sectioning the material in the fresh condition made it difficult to determine the extent of tylose formation, nevertheless numerous indications of these growths were found at the base of the old canes. Whether these occur in sufficient

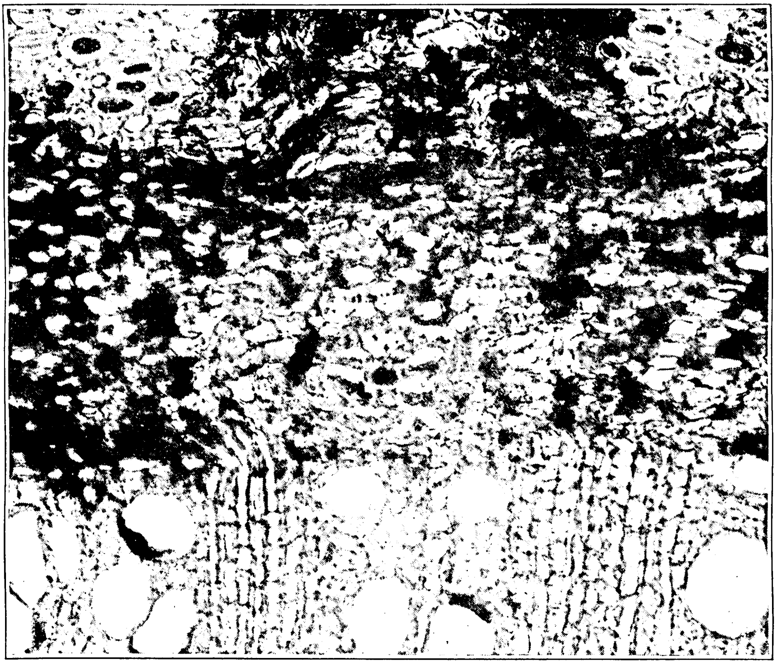

Fig. 21. Cross-section from the Base of a Ranere Cane Cut in January After the Fruiting Season. Complete Breakdown of the Phloem in the Dead Cane. ×435

numbers to interfere with water conduction has not been determined. Marshall (19) in some unpublished studies has shown that more water under moderate pressure may be forced through portions of old canes than through similar portions of new canes, but he has not shown that this greater rate of flow occurs in the normal water conduction of the old cane. Observations of the behavior of the tip region of old canes in the field indicate a deficiency in the water supply as shown by weak growth, small size of fruit, and early withering. Whatever the facts may be in relation to the water supply of the tip region, it is evident that the phloem of this portion of the cane declines at about the same time as that at the base.

Whether the degeneration of the phloem causes the decline of the old cane or vice versa has not been determined, but it is evident that phloem decline is at least associated with the death of the old cane. As phloem is known to be a relatively short-lived tissue and as the cambium in the old cane has been shown to be feeble, producing very little new phloem in the second year, it is possible that phloem decline in the raspberry cane is another expression of senility in the cambium.

Further evidence of decline in the phloem has been obtained through chemical analyses made in another phase of these studies of the raspberry cane. Some unpublished results of analyses made after harvest and in late November show the presence of reducing sugars in some quantity as the old cane declines and dies. These sugars were found to be more abundant in the central and upper regions of the cane than at the base and in somewhat greater concentrations in the laterals than in the cane. The presence of reducing sugar, a form of food easily transported in the normal living plant, suggests that the phloem which normally transports such food substances has declined in its activities. From such evidence it appears probable that there is little transport of elaborated foods to the root from the old cane after the harvest season, and that removal of the old cane at this time results in little or no loss of food supply to the roots.

BEHAVIOR OF STEM CUTTINGS

There have been very few reports of successful propagation of the red raspberry by means of stem cuttings and the successes reported have been with a hybrid form. Darrow (5) reported for the Van Fleet variety, a hybrid of *R. inominatus* x *R. strigosus,* the successful use of 2- and 3-eye cuttings buried an inch deep in flats provided with bottom heat in a greenhouse. Zimmerman (30) found that this variety could be propagated also by means of cuttings made from the new laterals early in the spring, but later[2] stated that old shoots did not respond similarly. In the present studies little or no success has attended efforts to propagate the Cuthbert and Latham varieties by means of cuttings.

Hardwood cuttings, made in January, 1929, from the basal, central, and apical regions of both vigorous and weak canes of the Cuthbert variety, were packed in moistened acid peat and kept in storage at 36° to 45° F. Under similar conditions cuttings of some plants such as grape and currant usually callous more or less freely, but after 17 weeks none of these raspberry cuttings showed even a trace of callous formation and no roots were developed.

Similar cuttings of the Latham variety were made in January, 1930, and placed in a cutting bed provided with bottom heat in a cool greenhouse. Comparable lots were placed in basic sand, in acid peat, and in a mixture of acid sand and acid peat. A few cuttings of the Beta grape and of a red currant variety were placed with each lot for comparison. When examined after 33 days most of the grape and currant cuttings were found to be well established or well calloused. None of the raspberry cuttings had rooted and only 14 per cent showed evidence of callousing. This callous formation generally was very

[2] Personal correspondence, 1930.

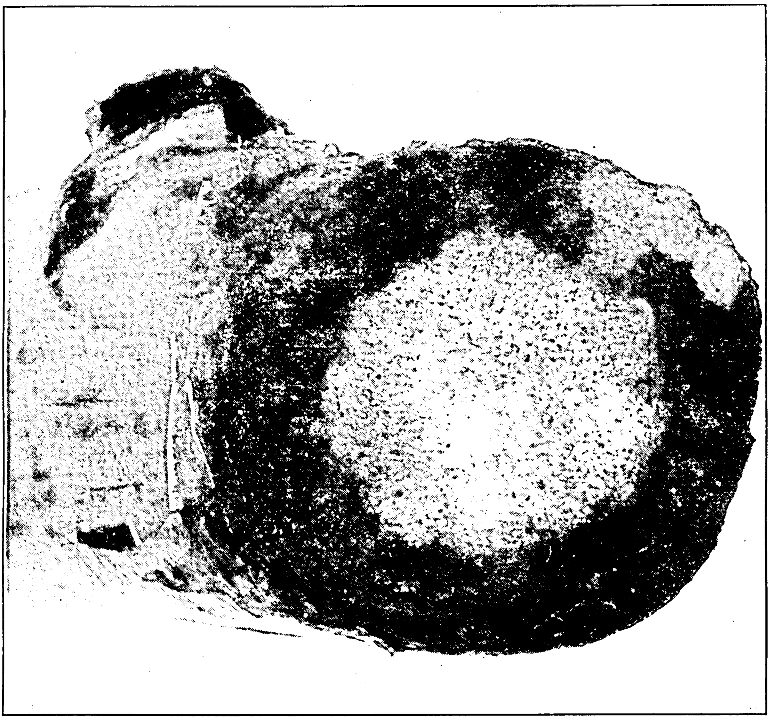

Fig. 22. Base of a Hardwood Cutting Made in January, 1930, from a Young Cane of Latham. After 33 days with Bottom Heat, Callous Formation Was Very Limited. ×5

feeble and at times was limited to a development on one side of the base of the cutting, as shown in Figure 22. More of those set in acid peat showed this feeble callousing than was the case in the other media, but all were failing rapidly. These data are given in Table IV. Altho the number of cuttings of each kind was not large the results as given in Table IV show that no regeneration of roots occurred in the red raspberry under conditions which brought about ready rooting in the grape and currant.

When sections were made of the cuttings which showed a feeble development of callous tissue, no indication of activity was found in the cambium at the proximal ends. Apparently the cambium in hardwood cuttings of the red raspberry does not respond as in the species studied by Sledge (26).

Some studies were also made relative to the callousing and rooting of green-wood cuttings of the Cuthbert and Latham varieties. Acid peat was used as the cutting bed medium and 200 cuttings of each variety were made in late April from the tips of young "suckers," which had grown 2 to 3 inches above the ground. Altho the losses

TABLE IV

CALLOUSING AND ROOTING OF HARDWOOD CUTTINGS OF RED RASPBERRY, GRAPE, AND RED CURRANT

Cutting bed medium	Latham raspberry	No.	Beta grape	No.	Red currant	No.
Basic sand	Leaves well developed, slight callous growth, no roots	1	Buds pushing, well calloused, rooting freely	7	Leaves well developed, well calloused, rooting freely	9
	Leaves withering, no callus, no roots	32	Buds pushing, well calloused, no roots	1	Buds dormant, well calloused, rooting freely	1
	Buds dormant, no callus, no roots	3	No bud activity, no callus, no roots	2		
Acid sand and acid peat	Weak bud activity, slight callous growth, no roots	1	Buds pushing, well calloused, rooting freely	10	Leaves well developed, well calloused, rooting freely	6
	Leaves withering, no callus, no roots	34			Buds swelling, well calloused, short root	1
	Buds dormant, no callus, no roots	2			Buds dormant, well calloused, no roots	3
Acid peat	Leaves withering, slight callous growth, no roots	13	Buds pushing, well calloused, rooting freely	9	Leaves well developed, well calloused, rooting freely	7
	Leaves withering, no callus, no roots	17			Buds pushing, well calloused, no roots	3
	Buds dormant, no callus, no roots	7				
		Per cent		Per cent		Per cent
Total rooting	0	0	26	90	24	80
Total callousing	16	14	1	3	6	20
Total failures	95	86	2	7	0	0

from damping off were heavy, in 12 days some feeble development of callous tissue was found in slightly less than half of the cuttings. In 33 days all of the Cuthbert and nearly all of the Latham cuttings had damped-off, but 9 fairly well rooted survivors remained among the Latham cuttings. This behavior suggests the possibility that a larger number of Latham cuttings would have rooted under more favorable conditions.

Another lot of cuttings was made from the tips of young canes of the Latham variety in late July, the canes at that time averaging 5 feet to 6 feet in height. These cuttings were set in acid peat in flats and kept outdoors in the shade. For 15 days they remained in good condition, but soon began to dry up or damp-off. Only 2 out of 200 cuttings showed any indications of callous formation and in these the callousing was very limited in extent.

Altho these studies of the callousing and rooting of raspberry stem cuttings were not extensive, they serve to indicate a very feeble response in the direction of regeneration of roots in the red raspberry. This response was more evident in the cuttings taken from very young suckers. By the end of July the response had declined markedly. In hardwood cuttings made from dormant young canes callousing was very feeble and no roots were formed. Priestly and Swingle (22) state that new root initials, when formed, are always found in tissues in close association with an active cambium. In view of this statement the fact that a few roots were formed on cuttings made from young suckers, but none on cuttings made later, seems to indicate that cambial activity declines in the cane during the first season and is feeble in the old cane. Evidence of this nature closely parallels that of the internal anatomy of the cane with regard to the behavior of the cambium.

CONCLUSIONS

The evidence obtained from these studies leads to the conclusion that the cambium in the red raspberry cane begins to decline in meristematic activity in the first season and is relatively feeble in the old cane. The apical meristem ceases to function at the end of the first season, no new winter buds are formed in the second year, and the cambium in the old cane forms relatively small amounts of new xylem and phloem elements. The evidence relating to the feebleness and decline of tissues within the old cane is in harmony with the decline of the cane as a whole, which has long been recognized by workers in the fields of botany and horticulture.

SUMMARY

Measurements of new and old canes show that there is an increase in diameter in the central and tip regions in the second year, but in 90 per cent of the old canes there is no measurable increase in diameter at the base.

The cambium during the first winter appears to be in a resting condition.

Cambial activity, as in other woody stems, is associated with the growth of new shoots.

Cambial activity, as shown by the formation of new xylem, probably occurs in nearly all growing canes in the second season. This activity in general is comparatively feeble and appears to be related to the vigor of the laterals and not to the vigor of the cane in the first year.

The formation of new xylem in the old cane does not appear to begin until the shoots have developed several leaves. In weak canes this activity is delayed and at times no new xylem is formed.

Cambial activity progresses downward slowly from the point of bud insertion and may be limited to the same side of the cane on which the shoot is growing.

Where the laterals are widely spaced on the cane the stimulus from the growing shoot does not appear to progress very far down the cane. In such cases the formation of new xylem may not occur 5 cm. below the shoot.

The limited development of new xylem at the base of the lateral usually results in a very weak attachment to the old cane and the lateral is easily broken off.

Where the laterals are numerous and fairly close together the cumulative stimulus from their growth results in general activity of the cambium and a complete tho narrow ring of new xylem is formed.

Apparently the stimulus from developing laterals does not extend downward far enough to cause the development of new xylem at the base of the average old cane, and there is usually no increase of diameter in that region of the cane.

Where vigorous laterals develop fairly close to the base of the old cane new xylem is formed. In some cases of this kind a complete ring of new xylem is formed. This explains the observation that in about 10 per cent of the old canes new xylem in varying amounts has been found at the base.

Cambial activity in neighboring areas between the large aggregate rays may not proceed at a uniform rate and some of these areas appear to cease growth earlier than others. This behavior suggests an early senile decline in the cambium.

Cambial activity in the second year is limited in some instances to the maturing of phloem initials cut off from the cambium late in the first year and to an increase in radial diameter of the remaining cambial cells. This condition is commonly found in the basal region of the old cane.

In the old cane, at about the height of the harvest season, discoloration of the phloem at the base of the cane indicates a breakdown of this tissue. Degeneration usually is more advanced in the basal region of the cane than in the central region. This degeneration is thought to be associated with the senile condition of the cambium.

Degeneration of the phloem in the apical region of the old cane, which is found to occur at about the same time as in the basal region, is believed to be caused by some disturbance in the water conduction in the old cane.

Studies of stem cuttings with regard to callous formation and regeneration of roots indicate that a decline in meristematic activity begins early in the first year.

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